THE GENERA OF GUTTIFERAE (CLUSIACEAE) IN THE SOUTHEASTERN UNITED STATES [1]

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GUTTIFERAE A. L. de Jussieu, Gen. Pl. 255. 1789, nom. cons.

Trees, shrubs, subshrubs, or perennial or annual herbs with translucent or black secretory cavities present as dots or elongate sacs; sap resinous, yellow [white or greenish] or clear and colorless. Leaves opposite, simple, entire, exstipulate. Flowers perfect or imperfect (the plants then dioecious [or polygamous]), often showy, regular, hypogynous, in simple or compound dichasia or rarely solitary. Sepals 4 or 5[–10], when 5, quincuncially imbricate (*2* outside, *2* inside, 1 in and out). Petals 4 or 5 to 9[10], yellow, flesh-colored, greenish, or pink to white, usually asymmetrical, convolute or imbricate vertically in the bud. Androecium of numerous to few stamens, filaments elongate, distinct or united at base [or throughout], staminodia present or absent; pollen usually 3-colporate. Gynoecium of [1] 2–9[–15] united carpels; styles as many as carpels, closely connate or free and divergent, or stigmas sessile; stigmas capitate or minute, or large and flat in *Clusia*; ovary superior, placentation axile, pseudoaxile, or parietal; ovules numerous to few [or one], anatropous, 2-integumented. Fruit a septicidal capsule [berry or drupe]. Seeds small [to large], the raphe inconspicuous or forming a keel, an aril present or absent; embryo straight; endosperm lacking. (Clusiaceae Lindley, Nat. Syst. ed. 2. 74. 1836, nom. alt. cons. Including Hypericaceae A. L. de Jussieu, Gen. Pl. 254. 1789, nom. cons.; type genus: *Hypericum* L.)
TYPE GENUS: *Clusia* L.

[1] Prepared for the Generic Flora of the Southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation, currently under Grant BMS74–21469 (Carroll E. Wood, Jr., principal investigator). This treatment follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area; supplementary information is included in brackets. References that neither author has verified are marked with an asterisk.

We are indebted to George Avery for his data on the distribution of *Clusia rosea* in the Florida Keys and to W. T. Gillis and P. B. Tomlinson for additional comments on this species as it occurs in southern Florida. The illustration of *Clusia* was drawn by Karen S. Velmure under the supervision of Kenneth R. Robertson, who noted the occurrence of polyembryony in material collected by him and C. E. Wood, Jr., in the Fairchild Tropical Garden, Miami, Florida. The illustration of *Triadenum* is the work of Rachel A. Wheeler and is based largely on materials collected by C. E. Wood, Jr. Beverly Vincent assisted with the preparation of the typescript and part of the bibliography.

A family of about 50 genera and some 900 species chiefly of the tropics and subtropics of both hemispheres. *Hypericum* L. and *Triadenum* Raf. are widely distributed in our area; *Clusia* L. reaches it only on the Florida Keys.

Engler (1925) considered the Guttiferae to comprise five subfamilies (ten tribes), with *Clusia* in subfam. Clusioideae and *Hypericum* and *Triadenum* in subfam. Hypericoideae. Melchior adopted the same classification but added a sixth subfamily to accommodate *Lorostemon* Ducke. Other authors (e.g., Lawrence, Gleason, Hutchinson, Takhtajan) have elevated subfam. Hypericoideae to the rank of family (Hypericaceae). From studies of the comparative anatomy of the Guttiferae, the Hypericaceae, and related families, Vestal found that the Guttiferae do not differ significantly from the arborescent members of the Hypericaceae. He concluded that it is a matter of opinion whether the two taxa are considered as separate families or as a single family. After an intensive investigation of the floral anatomy, Robson concluded that Engler's subfam. Hypericoideae cannot be given familial status without dismembering the Guttiferae completely and recognizing all the other subfamilies as families, a clearly undesirable course because of the close interrelationships of these subfamilies. Robson concluded further that subfam. Hypericoideae is related to subfam. Clusioideae through *Vismia* Vandelli and to subfam. Calophylloideae through *Hypericum*.

As the name Guttiferae suggests, a distinguishing characteristic of this family is the presence of secretory cavities and/or canals throughout most of the plant body. In many arborescent members these secretory receptacles are filled with a white, yellow, or greenish resinous sap. A clear resinous sap, especially noticeable in the shrubby species of sect. MYRIANDRA, is present in many species of *Hypericum*. The secretory cavities of many of the herbaceous members of *Hypericum*, especially those of sect. HYPERICUM, have a black pigment.

The Guttiferae seem to be closely related to the tribe Bonnetieae of the Theaceae, and the two families may have evolved from a common ancestral stock.

In our area the Guttiferae are of little economic importance. A few of the shrubby species of *Hypericum* have occasionally been cultivated for ornament. Fourteen species of *Hypericum* from the Old World are listed by Bailey as being in cultivation in the United States and Canada. The European *H. perforatum* L., poisonous to farm animals, is a noxious weed, especially in western North America and Australia. In the West Indies *Garcinia Mangostana* L., mangosteen, $2n = 76$, and *Mammea americana* L., mamee apple, *mamey amarillo*, *mamey de Santo Domingo*, are highly prized for their edible fruits. *Mammea* is cultivated to some extent in southern Florida. Experimental plantings of the mangosteen have been made in southern Florida, but this strictly tropical fruit has not yet been a success. Moderate success has been achieved with a few other species of *Garcinia*, including *G. Livingstonei* T. Anderson.

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KEY TO THE GENERA OF GUTTIFERAE IN THE SOUTHEASTERN UNITED STATES

General characters: *plants with translucent or black secretory cavities present as dots or elongate sacs; sap resinous, yellowish, greenish, or clear; flowers perfect or imperfect, regular, hypogynous, 4- or 5-merous, usually in simple or compound dichasia; stamens numerous to few, distinct or united at base; gynoecium 2–10-carpellate; ovules anatropous; placentation axile, pseudoaxile, or parietal; fruit a septicidal capsule.*

A. Leaves thick, leathery, obovate, rounded or emarginate at apex, cuneate at at base; tree with viscid yellow sap; flowers imperfect; seeds arillate. . . . . 1. *Clusia.*

A. Leaves various, not as above; sap clear, not yellow; flowers perfect; seeds not arillate.

B. Petals yellow; staminodia lacking; stamen fascicles (when present) consisting of an unequal number of stamens; herbs, shrubs, or small trees. . . . . 2. *Hypericum.*

B. Petals flesh-colored, pinkish, or greenish; stamen fascicles 3, consisting of 3 stamens each, alternating with 3 staminodia; herbs. . . . . 3. *Triadenum.*

Subfam. CLUSIOIDEAE [Engler in Martius & Eichler, Fl. Brasil. **12**(1): 393. 1888.]

Tribe CLUSIEAE [Choisy in DC. Prodr. **1**: 557. 1824.]

1. **Clusia** Linnaeus, Sp. Pl. **1**: 509. 1753; Gen. Pl. ed. 5. 226. 1754.

Trees or shrubs, often epiphytic or half climbing on other trees and sometimes strangling them, with a viscid resinous yellow [or white] sap that flows from every part when cut. Leaves thick, leathery, rigid. [Inflorescences cymose or] flowers solitary and terminal. Flowers imperfect [? rarely perfect], the plants dioecious [or seldom polygamous]. Sepals 4[–6]. Petals [4–]6–9[–10], white or rose-colored. [Staminate flowers: stamens numerous, filaments united at base (or throughout), inner stamens often staminodial; gynoecium rudimentary or lacking.] Carpellate flowers: staminodia [5 to] many, united in a ring around the ovary [or free]; gynoecium of [5–]6–9[–10] carpels; styles short and thick or lacking; stigmas radiating; ovules numerous in each locule. Fruit thick, leathery or fleshy, subglobose in ours, capped by the persistent stigmas, at length capsular, dehiscent into as many valves as stigmas. Seeds inclosed in a fleshy aril; outer seed coat fleshy, inner seed coat leathery; cotyledons much reduced, the embryo consisting largely of radicle. LECTOTYPE SPECIES: *C. major* L. (*C. alba* Jacq.); see N. L. Britton, N. Am. Trees 700. 1908. (Name commemorating Charles de l'Écluse [Carolus Clusius], 1525–1609, author of *Rariorum plantarum historia.*) — BALSAM APPLE, PITCH APPLE.

A genus of perhaps 100–200 species of the New World tropics and subtropics. In the most recent outline of the genus Engler (1925) recognized two subgenera and 17 sections. The taxonomy of the group is

difficult, herbarium specimens are in many ways unsatisfactory for study, and dioecism poses additional problems.

Clusia rosea Jacq., of subg. CLUSIA (subg. *Thysanoclusia* Vesque), sect. CHLAMYDOCLUSIA (Engler) Engler, is the only representative of the genus in the United States, where it is a rare plant on some of the Florida Keys. Reports of *C. flava* Jacq., of sect. CLUSIA (sect. *Stauroclusia* Planchon & Triana), from Key West are unsubstantiated, specimens so labeled being *C. rosea* instead (cf. Howard, 1962, p. 393). *Clusia flava* appears to be restricted to Grand Cayman and Jamaica. *Clusia rosea* is a Caribbean plant distributed from the Virgin Islands through the Greater Antilles to the Bahamas and southernmost Florida. In Florida it was first collected at Key West (where it was long ago exterminated), and it has since been found on Sugarloaf, Cudjoe, Little Torch, Big Pine, No Name, and Bahia Honda keys, Monroe County, *fide* George Avery, who notes that with the exception of the stations on Big Pine and No Name keys, all of these localities are immediately adjacent to former habitations. The plant is also known as an introduction on Key Biscayne, Dade County. *Clusia rosea* is nowhere frequent on the Keys, and in at least some of these localities all of the plants appear to have been removed or destroyed. With the ever-increasing alteration of the Florida Keys by man, it is problematical whether this species will survive there as a wild plant.

Under more favorable conditions than those in the Keys, *Clusia rosea* may become a tree up to 20 meters tall. It often begins as an epiphyte and grows like a strangling fig (*Ficus*). It is easily recognized by the very thick, leathery, obovate leaves that are either rounded or emarginate at the apex and cuneate at the base; by the copious yellow sap; and by the large, usually solitary flowers with six to nine white petals marked with pink. The plant is a handsome ornamental and is frequently cultivated in southern Florida, where only carpellate individuals seem to be present. Carpellate specimens set abundant fruit, however, and have viable seeds, embryos evidently being produced apomictically. Van Tieghem (1885) noted one to three embryos in seeds of *C. rosea*, and Vesque (1893, p. 110) found that seeds from a fruit that he examined were all polyembryonic. Seeds from a tree in the Fairchild Tropical Garden in Miami are also polyembryonic (see FIGURE 1, m, o, p). The distribution and frequency of staminate plants in the West Indies is very uncertain, but they appear to be rare or uncollected. None are represented in the collections of the Arnold Arboretum and the Gray Herbarium (but see Little & Wadsworth, 1964, under family references).

In carpellate flowers of *Clusia rosea* the numerous staminodia are almost completely fused together in a ring around the ovary. At anthesis they begin to deliquesce from the tips downward into a sticky, brownish, opaque mass that attracts bees. Both the conspicuous aril around the seed and the fleshy outer seed coat are bright orange, and the seeds are undoubtedly bird-dispersed. The embryo is notable for the greatly reduced cotyledons and relatively large radicle (cf. FIGURE 1, m).

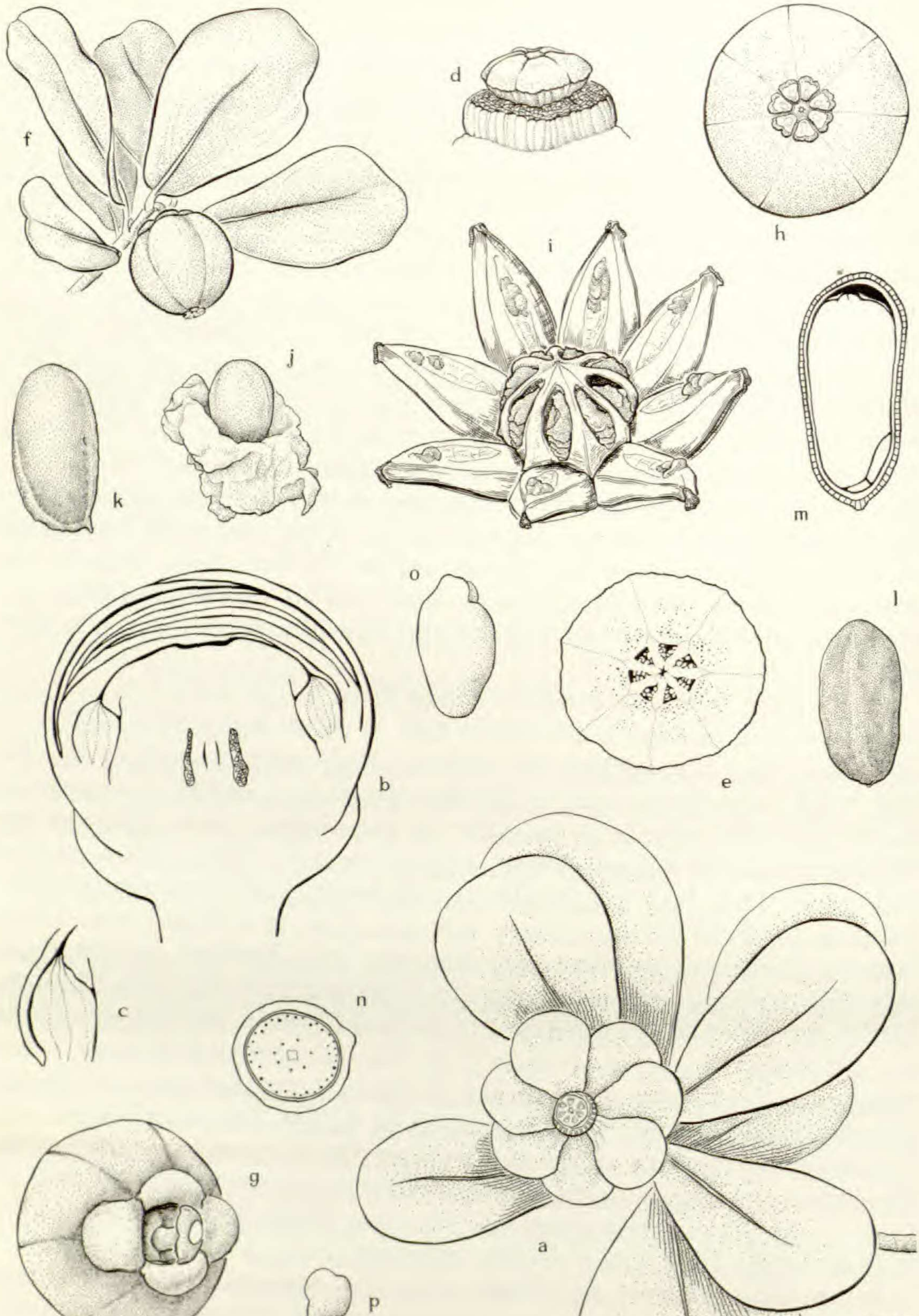

FIGURE 1. **Clusia.** a–p, *C. rosea,* carpellate plant only: a, branch with carpellate flower, × ¼; b, vertical section of carpellate flower bud — note overlapping petals, phalanges of staminodia to either side of ovary, numerous ovules in each locule of ovary, × 2; c, detail of "b" to show four rows of staminodia, × 3; d, gynoecium surrounded by staminodia — gummy, deliquesced upper

Collectors of *Clusia* species should note the color of the sap (yellow or white) that oozes from cut surfaces, for this characteristic is supposed to delimit major groups of species. Efforts should also be made to obtain specimens from both staminate and carpellate plants. No chromosome counts have been recorded for any member of the genus.

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part of staminodia removed (dissolved away with alcohol), × 1; e, cross section of ovary from older flower to show placentation — note numerous secretory ducts in ovary wall, × 2; f, branch with nearly mature fruit, × ¼; g, underside of unopened fruit with accrescent sepals (4) and pair of bracts at base of peduncle, × ½; h, fruit from above to show persistent accrescent stigmas, × ½; i, open capsule with arillate seeds, some near tips of woody valves, most stacked in locules, × ½; j, seed with aril, × 3; k, seed, outer seed coat fleshy, × 4; l, seed with outer coat removed, × 4; m, diagrammatic vertical section of polyembryonic seed, fleshy outer seed coat hatched, mature embryo with greatly enlarged radicle and small apical cotyledons filling most of seed, two much smaller embryos at lower right, × 6; n, cross section of seed through radicle of embryo — note numerous secretory ducts, × 6; o, smaller embryo from "m," radicle enlarging, × 12; p, smallest embryo from "m," × 12.

Subfam. HYPERICOIDEAE Engler in Martius & Eichler,
Fl. Brasil. **12**(1): 391. 1888.

Tribe HYPERICEAE Choisy, Prodr. Monogr. Fam. Hyperic. 37. 1821.

2. **Hypericum** L. Sp. Pl. **2**: 783. 1753; Gen. Pl. ed. 5. 341. 1754.

Small trees, shrubs, subshrubs, perennial or annual herbs, generally lacking pubescence. Leaves sessile or clasping, elliptic, oblanceolate, narrowly linear or needlelike, with or without an articulation at base. Inflorescence usually a simple or compound dichasium; flowers perfect, sepals 4 or 5, rarely 3 or 6, persistent long after fruit maturity or deciduous at capsule dehiscence. Petals 4 or 5, rarely 3 or 6, yellow, convolute in the bud, deciduous soon after anthesis or long-persistent as withered remains. Stamens numerous, or only 5–10 (in small-flowered species), in 3 or 5 fascicles or the filaments united at their bases to form a shallow ring or narrow band, deciduous or persistent, staminodia present or absent. Gynoecium of 5 (4, 3) or 2 carpels; ovary ovoid, gradually contracted into a stout persistent style, unilocular or partially divided by intruding placentae, or completely 3–5-locular. Capsule globose, ovoid or conic. Seeds short-cylindric; seed coats finely to coarsely reticulate, occasionally obscurely striate. (Including *Ascyrum* L., *Crookea* Small, *Sarothra* L., and *Sanidophyllum* Small.) LECTOTYPE SPECIES: *H. perforatum* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. **2**: 529. 1913. (*Hyperikon*, an ancient Greek name, probably for a species of this genus.) — ST. JOHN'S-WORT.

A genus of some 300 species of the subtropics, the highland areas of the tropics, and the warmer regions of the temperate zones. Represented in our area by about 40 species.

Hypericum, as delimited in this treatment, is broadly conceived to include *Ascyrum*, *Sarothra*, *Crookea*, and *Sanidophyllum*. Support for this concept of the genus comes from intensive studies by Robson and by Adams on the floral anatomy and taxonomy of *Hypericum*, various generic segregates, and related genera.

A satisfactory infrageneric taxonomy of *Hypericum* has been most difficult to achieve. Traditionally, flower structure has been used, especially the presence or absence of staminodia and the degree of fasciculation of the stamens. Using these and other characters, Keller (in Engler, 1925) recognized 18 sections within the genus (as delimited by him). Three of these, sect. HYPERICUM, sect. BRATHYS (Mutis ex. L. f.) Choisy, and sect. MYRIANDRA (Spach) Endl., are represented in our area. A fourth, sect. BRATHYDIUM (Spach) Endl., has been united with sect. MYRIANDRA by Adams.

Section HYPERICUM is represented in our area by the indigenous *H. punctatum* Lam., *H. Mitchellianum* Rydb., *H. graveolens* Buckley, and *H. pseudomaculatum* Bush and by the introduced and widely naturalized *H. perforatum* L. Members of this section have black dots and lines in

their leaves, sepals, and petals; stamens connate at the base into three or five fascicles; capitate stigmas; and three separate styles that are strongly divergent from the base.

Perhaps the best known of these species is *Hypericum perforatum*, $2n = 32$, a European plant that was first reported in the United States from near Lancaster, Pennsylvania, in 1793. In our area this plant is merely a somewhat bothersome weed in pastures and old fields and along roadsides, but in some of the Western States, especially in northern California, "Klamath weed" becomes a noxious pest on rangelands. The plants contain a photodynamic red pigment, hypericin, a napthodianthrone derivative, which if eaten by livestock sensitizes the white areas of the animal's skin to sunlight. Affected animals often develop body sores, swollen ears, and sore muzzles, and their weight and vigor are greatly reduced. Considerable progress has been made in the biological control of *H. perforatum*, especially by several species of beetles of the genus *Chrysolina* that have been introduced from Europe specifically for this purpose. These beetles feed on the plants, eventually killing them. The same control measures have been used successfully in Australia. Abundant seed production (an average of more than 23,000 seeds per plant) and prolific vegetative reproduction by both crown and root sprouts contribute to the aggressive weedy nature of *H. perforatum*. Apomixis has been discovered in European populations.

The 16 chromosomes of *Hypericum punctatum* and of *H. Mitchellianum* show ring formation of the *Oenothera* type at meiosis, a chromosomal behavior that is often a sign of structural hybridity. The closely related *H. graveolens* and *H. pseudomaculatum* are apparently normal cytologically.

Section BRATHYS is represented in our area by about 11 species of annual or perennial herbs belonging to subsect. SPACHIUM Keller. Members of this section are characterized by translucent glands in leaves, sepals, and petals; stamens generally fewer than 20 and arranged in three to five obscure groups; styles separate to the base and widely divergent at anthesis; and capitate stigmas. A striking member of this group is *Hypericum setosum* L., a plant of wet pinelands on the Coastal Plain from Louisiana to southeastern Virginia and the only hairy *Hypericum* in North America. Another interesting species of sect. BRATHYS, *H. cumulicola* (Small) P. Adams, the single species of *Sanidophyllum*, is a wiry herbaceous perennial known only from the *Pinus clausa* scrub of Highlands County, Florida. In its morphology and ecology, it seems to be most closely related to *H. gentianoides* (L.) BSP. (*Sarothra gentianoides* L.), which occurs over much of the eastern United States and disjunctly in Belize (*H. aphyllum* Lundell) and Brazil. It is clear that *H. cumulicola* represents merely an extreme evolutionary development within the section. Similarly, *H. gentianoides* and *H. Drummondii* (Grev. & Hooker) Torrey & Gray, closely related annuals of eastern North America assigned by Small to *Sarothra*, are clearly members of sect. BRATHYS allied to the *H. canadense–H. denticulatum* complex.

Two different chromosome levels are known in sect. BRATHYS in eastern North America. A diploid number of 16 occurs in *H. boreale* (Britton) Bicknell, *H. mutilum* L., *H. majus* (Gray) Britton, and *H. canadense* L., while *2n* equals 24 in *H. gentianoides* and *H. denticulatum* Walter. Counts are needed for the other species of the section.

Intensive study of sect. BRATHYS is needed for a satisfactory delimitation of the species. Many of the taxonomic difficulties may be the result of extensive hybridization. According to Fernald, *H. mutilum* hybridizes with *H. gymnanthum* Engelmann & Gray, *H. majus*, and *H. canadense*, while *H. canadense*, in turn, crosses with *H. boreale* and *H. majus*. Fernald suggested that *H. dissimulatum* Bicknell is "perhaps an unusually constant and recurrent hybrid" of *H. canadense* with either *H. boreale* or *H. mutilum*.

Section MYRIANDRA is represented in our area by about 30 species of trees, shrubs, and herbaceous perennials. Plants of this section have styles that are closely appressed along their entire length at anthesis, minute stigmas (i.e., noncapitate ones), and translucent secretory cavities (dots or elongate sacs) throughout the plant body.

The taxonomy of sect. MYRIANDRA has been altered considerably by Adams, who has extended the limits of subsect. CENTROSPERMA Keller (in Engler, 1895) to include nearly all of the species of subsect. SUTUROSPERMA Keller. Thus enlarged, subsect. CENTROSPERMA includes 15 species of shrubs that have leaves and sepals with an articulation or groove at the base. Subsection SUTUROSPERMA has been altered to include the remnants of Keller's original subsection, plus the species formerly assigned to sect. BRATHYDIUM (Spach) Endl. and those placed in *Ascyrum* and *Crookea*: *H. stans* (Michx.) Adams & Robson (*Ascyrum stans* Michx.), *H. Edisonianum* (Small) Adams & Robson (*A. Edisonianum* Small), *H. tetrapetalum* Lam. (*A. tetrapetalum* (Lam.) Vail), *H. Hypericoides* (L.) Crantz (*A. Hypericoides* L.), *H. stragulum* Adams & Robson (*A. multicaule* Michx.), *H. suffruticosum* Adams & Robson (*A. pumilum* Michx.), *H. microsepalum* (Torrey & Gray) Gray ex S. Watson (*Crookea microsepalum* (Torrey & Gray) Small). As thus delimited, subsect. SUTUROSPERMA includes 15 species of shrubs and perennial herbs, the leaves and sepals of which lack an articulation or groove at the base. The redefined sect. MYRIANDRA appears to be a very natural group, within which *Ascyrum* and *Crookea* are only extreme evolutionary developments.

One group of closely related species in sect. MYRIANDRA, the *Hypericum fasciculatum* complex, has long been difficult taxonomically. Within the group Adams has distinguished eight species, each with a distinctive geographic range and specific habitat requirements. These eight (*H. fasciculatum* Lam., *H. lissophloeus* P. Adams, *H. Chapmanii* P. Adams, *H. nitidum* Lam., *H. brachyphyllum* (Spach) Steudel, *H. reductum* P. Adams, *H. Lloydii* (Svenson) P. Adams, and *H. exile* P. Adams) most likely share a common ancestry. They appear to be related through *H. galioides* Lam. to *H. densiflorum* Pursh and other members of subsect.

CENTROSPERMA. Additional studies, especially of the anatomy of the leaves, bark, and wood, are needed for a full understanding of infraspecific variation and a better delimitation of the species.

Three members of this complex native to western Florida (*H. Chapmanii* [Wakulla–Liberty counties west to Santa Rosa County], *H. nitidum* [western Florida; Baldwin County, Alabama; southern Georgia; Lexington County, South Carolina; and Brunswick County, North Carolina], and *H. lissophloeus* [Bay and Washington counties, Florida]) are unusual in that they become small trees often three or four meters in height. The single treelike stem of *H. Chapmanii* is often 10–15 cm. in diameter, especially near the base, but much of the width is a long-persistent, soft, spongy bark which often reaches a thickness of 3 or 4 cm.

In twenty-four of the thirty species of sect. MYRIANDRA the diploid chromosome number is 18; the remaining six species have not yet been studied cytologically. This chromosome number is also recorded for several species of *Hypericum* in other sections in other regions of the world.

The flowers of several species of sect. MYRIANDRA are known to be pollinated by bumblebees, honey bees, and various kinds of smaller bees, which obtain pollen from the large number of stamens.

Several species of sect. MYRIANDRA are planted as ornamentals. *Hypericum Buckleyi* M. A. Curtis is valued as a rock-garden or ground-cover plant, while *H. frondosum* Michx. is grown for its large, showy flowers. *Hypericum prolificum* L. and *H. Kalmianum* are used as ornamentals, both for their showy flowers and their smooth, lustrous brown bark, which adds interest to the winter aspect of the garden. Other species of this section, including *H. densiflorum*, *H. lobocarpum* Gattinger, and *H. nudiflorum* Michx., are sometimes planted but are not well recommended.

Some hybridization appears to occur between species of sect. MYRIANDRA. *Hypericum lobocarpum* and *H. prolificum* are believed to hybridize occasionally where the ranges of the two overlap in central Arkansas. A highly variable population in a pasture at Highlands, North Carolina, may have originated from hybridization between cultivated plants of *H. prolificum* and *H. frondosum*. Some spontaneous hybridization may occur when two or more of these woody species are brought into the garden. Two such putative hybrids, *H.* × *Dawsonianum* Rehder (*H. lobocarpum* × *H. prolificum*) and *H.* × *arnoldianum* Rehder (*H. densiflorum* × *H. lobocarpum*) were discovered at the Arnold Arboretum of Harvard University (see Adams, 1972).

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3. Triadenum Rafinesque, Fl. Tellur. 3: 78. 1837.

Perennial rhizomatous herbs. Leaves sessile or petiolate, oblong, oblong-lanceolate or elliptic, without an articulation at base, lacking black secretory glands, but dotted with clear glands which often turn dark upon drying. Inflorescence dichasial. Flowers perfect. Sepals 5, nearly equal, persistent, without an articulation at base. Petals 5, imbricate (or intermediate between imbricate and valvate) in the bud, flesh-colored, pinkish, greenish [or white], never yellow, symmetrical, deciduous soon after anthesis. Androecium of 3 fascicles of 3 stamens each, alternating with 3 hypogynous glandular staminodia, the stamens persistent. Gynoecium 3-carpellate; styles 3, separate to the base and divergent; stigmas capitate; placentation axile; ovules numerous. Seeds cylindrical; seed coat finely reticulate; raphe inconspicuous, not forming a keel or wing. TYPE SPECIES: *T. virginicum* (L.) Raf. — MARSH ST. JOHN'S-WORT.

A genus of four or more species in eastern North America, eastern Asia (*Triadenum japonicum* (Blume) Makino [*Hypericum crassifolium* (Blume) Nakai, not *H. japonicum* Thunb.] and perhaps one or two others), and India (*T. breviflorum* (Wallich ex Dyer) Y. Kimura). It is represented in our area by four taxa that are treated either as species (Gleason) or as varieties of two species (Fernald): *T. virginicum* (L.) Raf. (*Hypericum virginicum* L.), $2n = 38$; *T. Fraseri* (Spach) Gleason (*H. Fraseri* Spach, *H. virginicum* var. *Fraseri* (Spach) Fernald); *T. tubulosum* (Walter) Gleason (*H. tubulosum* Walter, *T. longifolium* Small); and *T. Walteri* (J. F. Gmelin) Gleason (*H. tubulosum* Walter var. *Walteri* (J. F. Gmelin) Lott).

The species of *Triadenum* have long been assigned by most botanists to *Hypericum* sect. ELODEA (Juss.) Choisy, but several authors, including Holm, Small, and Gleason, have regarded this taxon as a distinct genus and have revived the long-unused Rafinesque name for it. As delimited by these workers, species of *Triadenum* differ from *Hypericum* in the petals, which are imbricate, rather than convolute, and pink to greenish, instead of yellow, and in the nine stamens in three fascicles of three each, with three alternating staminodia. Studies by Robson of the

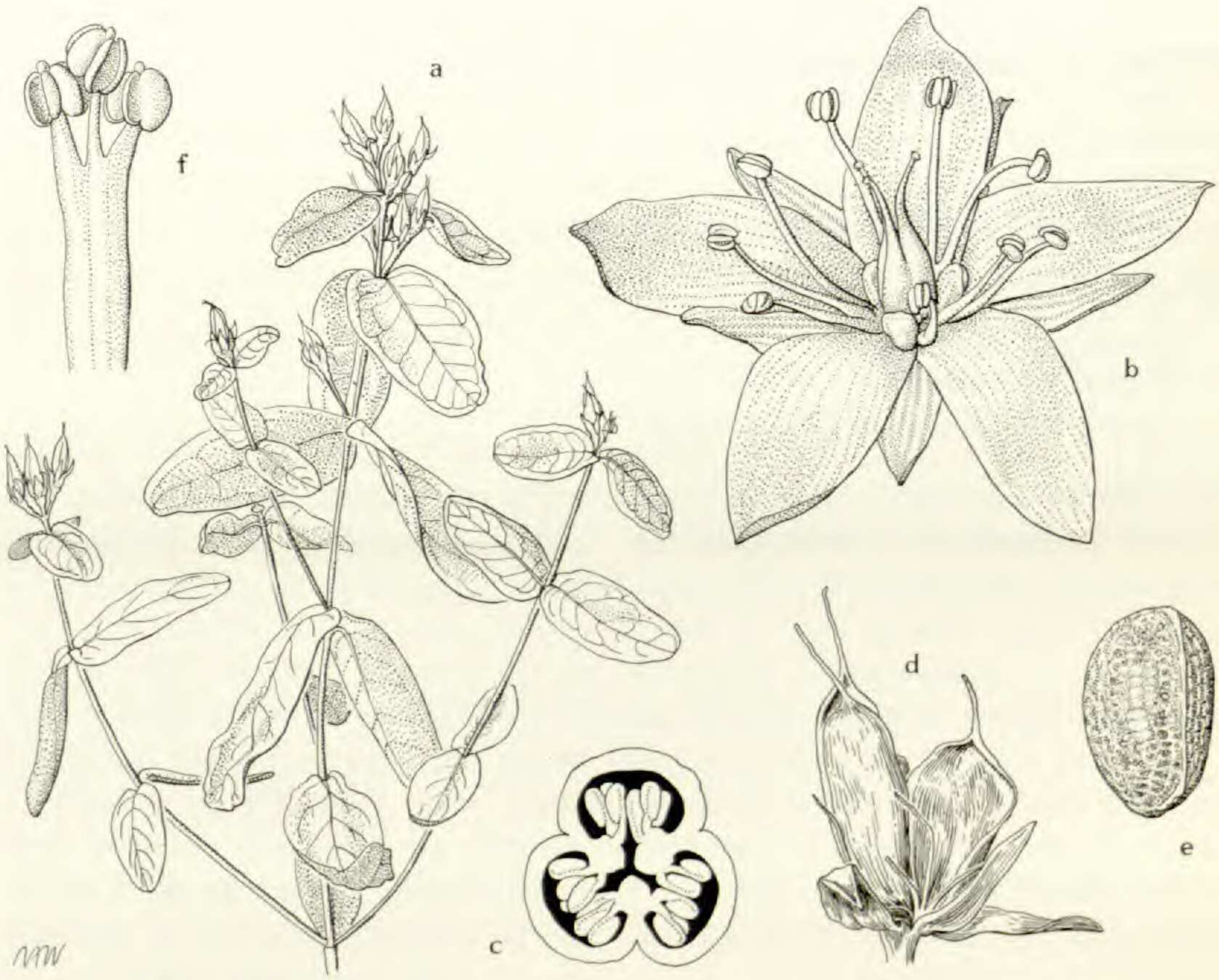

FIGURE 2. **Triadenum.** a–e, *T. virginicum*: a, upper part of plant with nearly mature fruit, × ½; b, flower — note stamens in three's with alternating staminodia, × 5; c, cross section of ovary to show placentation, × 15; d, capsule after dehiscence, × 3; e, seed, × 25. f, *T. Walteri* (*T. tubulosum* var. *Walteri*), fascicle of stamens — compare with "b," × 12.

vascularization of the flower strongly suggest that the group is indeed sufficiently distinct from *Hypericum* to warrant treatment as a separate genus. Robson concluded that the species of *Triadenum* are actually more closely related to *Cratoxylon* than to *Hypericum*. The floral anatomy of *Triadenum* closely resembles that of *Cratoxylon*, from which, in his opinion, it is an herbaceous derivative.

An intensive taxonomic study of *Triadenum* would aid greatly in understanding the delimitation of the species and the variation patterns within each species. Additional chromosome counts are needed. Studies of the reproductive biology would also be of value.

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